

## First Biological Data for *Aspilodemon* Fischer (Hymenoptera: Braconidae: Hydrangeocolinae): Parasitoids of Cecidomyiid Fly Galls on Asteraceae in Brazil

RUBENS A. M. ODA, MARGARETE VALVERDE DE MACÊDO, AND DONALD L. J. QUICKE

(RAMO, MVM) Laboratório de Ecologia de Insetos, Departamento de Ecologia, CP 68020, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro CEP 21941-590, Brazil; (DLJQ) Unit of Parasitoid Systematics, Department of Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K., and Department of Entomology, The Natural History Museum, London SW7 5BD, UK

---

*Abstract.*—Biological data for the hydrangeocoline braconid genus *Aspilodemon* Fischer are reported for the first time. An *Aspilodemon* sp. from Brazil is reported as a parasitoid of three species of *Liodiplosis* spp. (Diptera: Cecidomyiidae) which induce galls on leaves of the liana, *Mikania glomerata* (Asteraceae); it does not attack other gall-forming cecidomyiids on the same plant, and evidence suggests that it is ectoparasitic although direct observations of parasitoid larvae have not been made. How this affects our understanding of the evolution of gall formation and aphid parasitism by braconids is discussed.

---

The Hydrangeocolinae are a recently recognised subfamily of braconid wasps (Dowton et al. in press, Belshaw and Quicke in press), to date known from three genera, each with a southern distribution, viz *Hydrangeocola* Brèthes (= *Kephalosema* Fischer) from Chile, *Aspilodemon* Fischer, from Central and South America and *Opiopterus* Szépligeti (see Wharton 1993, Whitfield and Wharton 1997), from Australia. Until recently, some of these taxa were typically treated under the subfamily Opiinae (e.g. Fischer 1966, but see Wharton 1988) or more recently the Hormiinae, see e.g. Whitfield and Wharton (1997) or Rhyssalinae (Quicke et al. 1997) though several of these authors recognised, they do not fit well into any of these (see electronic appendix of Belshaw et al. 2000 for further discussion). Interest in the group was recently increased because molecular sequence data strongly indicate that they are not related to Opiinae, Hormiinae or Rhyssalinae, but instead form a sister group to the endemic Australian subfamily, Mesostoinae, and that together

these are the sister group of the well known Aphidiinae (Belshaw et al. 2000). This newly discovered relationship was particularly interesting as it appeared to suggest both a Gondwanan origin of the Aphidiinae despite their currently predominantly northern distribution, and a link with galls, because the most primitive extant aphids are gall formers, mesostoinae braconids form galls on *Banksia* spp. (Proteaceae) (Austin and Dangerfield 1998) and the only hydrangeocoline for which some biology is known, *Hydrangeocola*, has been reared from unidentified galls on *Hydrangea* (Hydrangeaceae) (Brèthes 1927). Very little is known, however, about the biologies of the putatively most primitive extant aphidiines, and a direct association of any these with gall-forming aphids is yet to be confirmed.

Here we present the first rearing data for the genus *Aspilodemon* based on a probably undescribed species from Brazil. The species concerned is associated with cecidomyiid fly galls on *Mikania glomerata* Sprengel, and the available evidence

Table 1. Number of galls collected in each locality during study; gall types are illustrated in Gagné et al. (2001).

Locality	Morphological type of gall						
	Cylindrical	Spherical	Conical	Leaf/Vein	Bud	Epidermis	Stem
Parati	2070	1085	0	885	5	53	27
Itatiaia	1385	468	0	574	11	17	22
Poço	1061	583	17	272	5	17	0
Picinguaba	861	471	188	305	2	38	9
S. Órgãos	297	361	0	252	2	20	56
Tijuca	0	6	824	51	0	141	0

strongly suggests that it is a parasitoid of the fly larva. *M. glomerata* is a liana species belonging to the Asteraceae, and it occurs inside and on the edges of forests, flowering from August to December. The genus *Mikania* has 415 species mainly distributed in Central and South America, of which 171 species occur in Brazil (King and Robinson 1987). *M. glomerata* ranges from north-eastern Brazil down to the southern-most part of Brazil and just into Argentina and Paraguay (Ritter et al. 1992).

### MATERIALS

Voucher specimens of the *Aspilodemon* sp. reared are deposited in each of the following collections: The Natural History Museum, London; the Entomological Collection of the Laboratório de Ecologia de Insetos, Department of Ecology, Universidade Federal do Rio de Janeiro. Morphological terminology follows Sharkey and Wharton (1997). The D2-D3 28S rDNA gene sequence for the species of *Aspilodemon* referred to here is deposited in EMBL: accession number AJ245685 (and has been used in phylogenetic analyses of Belshaw et al. 2000 and Quicke and Belshaw 1999).

*Study areas and sampling.*—The research was based in the Atlantic coast (Mata Atlântica) forests of Brazil which has one of the highest levels of biological diversity in the world, and is representative of humid tropical forests and their associated ecosystems (Mori et al. 1981). The localities were (1) Itatiaia National Park, Itatiaia

County, Rio de Janeiro State; (2) Serra dos Órgãos National Park, Teresópolis County, Rio de Janeiro State; (3) Tijuca National Park, Rio de Janeiro County, Rio de Janeiro State; (4) Parati County, Rio de Janeiro State; (5) Picinguaba State Park, Ubatuba County, São Paulo State; (6) Biological Reserve of Poço das Antas, Silva Jardim County, Rio de Janeiro State. Four collections of galls (one per season—one day in the field) were made at each of the first five of the above localities: April or May, 1998 (Autumn), July or August 1998 (Winter), October or November 1998 (Spring) and January or February 1999 (Summer). The sixth locality was sampled at monthly intervals from February 1996 to October 1997. Total numbers of each type of gall collected at each field site are given in Table 1.

Eight species of cecidomyiid flies form galls on *Mikania glomerata* in Brazil, and the galls of most of these can be distinguished on the basis of their morphology and location on the plant (Table 2) (see Gagné et al. 2001, in which gall types are also illustrated). Cecidomyiid galls were collected from *M. glomerata* plants at six localities and reared to discover what parasitoids might be attacking them. Some galls were dissected.

### OBSERVATIONS

*Rearings of Aspilodemon.*—Rearings are summarized in Table 3. The numbers of each type of gall collected at each locality (Table 1) are estimates of their relative

Table 2. Cecidomyiid fly galls found on *Mikania glomerata* (Asteraceae) with descriptions of gall location and type.

Super-tribe Cecidomyiidi
<i>Mikaniadiplosis annulipes</i> (Gagné)—leaf vein swelling
Tribe Clinodiplosini
<i>Liodiplosis cylindrica</i> Gagné—cylindrical leaf gall
<i>L. conica</i> Gagné—conical leaf gall
<i>L. spherica</i> Gagné—spherical leaf gall
Tribe Asphondyliini
<i>Asphondylia glomeratae</i> Gagné—vein swelling
<i>A. moehni</i> Skuravá—stem swelling
<i>Perasphondylia mikaniae</i> Gagné—bud gall
Super-tribe Lasiopteridi
Tribe Alycaulini
<i>Alycaulus globulus</i> Gagné—leaf epidermis swelling

abundance, and therefore it is clear that although the cylindrical gall type was more abundant by approximately a factor of 2 at the three localities from where most individuals of *Aspilodemon* were obtained (Parati, Picinguaba and Poço), the *Aspilodemon* demonstrated a clear preference for the spherical gall type which yielded proportionately far more wasps (Table 3).

Except for the only individual obtained from the leaf vein swelling or vein swelling (we could not differentiate these two gall types) at Picinguaba, all *Aspilodemon* individuals were obtained from the galls induced by species of *Liodiplosis*. As we collected and reared many galls it is possible that the individual supposed to have been obtained from leaf vein swelling or vein swelling is a contamination.

Numerous Chalcidoidea were reared from the three gall types attacked by *Aspilodemon*; at least 10 species from the conical leaf gall type alone (taking all localities and sampling dates into account). The importance of *Aspilodemon* as a parasitoid (in terms of parasitism rate) varied: it was the commonest parasitoid reared from the spherical and conical leaf galls and the fourth commonest in the cylindrical gall.

*Evidence that Aspilodemon is a parasitoid*

Table 3. Total *Aspilodemon* rearings from cecidomyiid galls on *Mikania glomerata* at each site.

Locality	Morphological type of gall			
	Cylindrical	Spherical	Conical	Leaf/Vein
Parati	19	65	0	0
Itatiaia	1	0	0	0
Poço	2	44	3	0
Picinguaba	4	9	2	1
S. Órgãos	0	2	0	0

and not a gall-former.—*Aspilodemon* individuals were always found inside Cecidomyiidae gall chambers, and all the types of gall found (Table 1) yielded cecidomyiid flies showing that no gall type yielded only *Aspilodemon* and no potential hosts. Further, the *Aspilodemon* species was associated with three morphologically different gall types which would not be expected if it was a gall inducer itself.

*Evidence that Aspilodemon may be ectoparasitic.*—*Aspilodemon* pupates inside a cocoon which occupies approximately half of the cecidomyiid chamber. All the endoparasitoids that were also reared (see above) pupated inside the cecidomyiid skin and we could find the cecidomyiid larval sternal spatula (a strongly sclerotised thoracic feature) within the galls after these endoparasitoids had emerged. When *Aspilodemon* parasitised the cecidomyiid no host remains could be found, perhaps indicating that the sternal spatula had been consumed.

## DISCUSSION

The discovery that *Aspilodemon* is associated with galls strengthens the possibility that this way of life is the norm for the subfamily Hydrangeocolinae. Previously published suggestions that *Aspilodemon* belongs to the Opiinae (Fischer 1966) have been superseded by both morphological (Wharton 1988, Whitfield 1993) and molecular phylogenetic analyses (Belshaw et al. 2000), which instead support a relationship with the Australian subfamily Mesostoinae and also with the Aphidiinae.

Several transitions to cecidogenesis have occurred in the Braconidae: Mesostoinae appear to be exclusively cecidogenic on *Banksia* species (Proteaceae) (Quicke and Huddleston 1989, Austin and Dangerfield 1998); the enigmatic genus *Monitoriella* Hedqvist produces galls on *Philodeudron* (Liliaceae) (Infante et al. 1995); several species of the doryctine genus *Alorhogas* Gahan (Macêdo and Monteiro, 1989; Marsh et al. 2000), and another doryctine, *Psenobolus*, is an inquiline in figs (Ramirez and Marsh 1996) and may be partly cecidogenic. Knowledge that at least some Hydrangeocolinae (precise biology of *Hydrangeocola* is still unknown) are specialist parasitoids of gall-forming Diptera while the closely related Mesostoinae are cecidogenic suggests that the latter biology could have evolved from the former, as has been suggested for cecidogenic Eurytomidae (Chalcidoidea). It would be interesting to know whether any hydrangeocolines have also made this transition.

We wish to emphasise that we have not yet obtained any strong evidence about whether *Aspilodemon* is ecto- or endoparasitic. Although no host remains were found in galls parasitised by this wasp, indicating that all the host cuticle had been consumed, it should be noted that most endoparasitic braconids (those belonging to the 'helconoid' and 'microgastroid' groups of subfamilies—see Belshaw et al. 2000), very often emerge from their hosts before pupation and have an external feeding phase (Shaw and Huddleston 1991, Shaw and Quicke 2000). So even if the sternal spatula has been consumed it does not necessarily mean that the parasitoid was not endoparasitic in its earlier instars.

*Aspilodemon* differs from *Hydrangeocola* in only one fixed character—the fore wing pterostigma is narrow but distinct from vein R1 in the latter, whereas there is no discernible pterostigma in the former. In addition, *Aspilodemon* always lacks fore

wing vein 2a, whereas it is present in most *Hydrangeocola*. Given that for both these characters, *Hydrangeocola* displays (at least most species) the putatively plesiomorphic state, it is likely that the species classified under *Aspilodemon* may simply be a derived group of species within a broader concept of *Hydrangeocola*.

## ACKNOWLEDGEMENTS

We would like to acknowledge Ricardo F. Monteiro (UFRJ) for helping during all phases of the work, Raymond Gagné for identifying and describing the Cecidomyiidae species, IBAMA and IEF/SP for authorization to collect in the Units of Conservation, CNPq for the scholarships to R.A.M. Oda and financial support.

## LITERATURE CITED

- Austin, A. D. and D. C. Dangerfield. 1998. Biology of *Mesostoa kerri* Austin and Wharton (Insecta: Hymenoptera: Braconidae: Mesostoinae), an endemic Australian wasp that causes stem galls on *Banksia marginata* Cav. *Australian Journal of Botany* 46: 559–569.
- Belshaw, R., M. Dowton, D. L. J. Quicke, and A. D. Austin. 2000. A Gondwanan origin for a group of principally north temperate aphid parasitoids. *Proceedings of the Royal Society, London B*. 267: 491–496. [and electronic appendix at <http://www.pubs.royalsoc.ac.uk/publish/pro-bs/rpbl442.htm>]
- Belshaw, R., E. Herniou, C. Gimeno, M. G. Fitton and D. L. J. Quicke. 1998. Molecular phylogeny of the Ichneumonoidea (Hymenoptera) based on D2 expansion region of 28S rDNA. *Systematic Entomology* 23: 109–123.
- Belshaw, R. and D. L. J. Quicke. In press. Assessing character transitions when estimates of phylogeny are uncertain: the evolution of koinobiosis on concealed hosts by ichneumonoid parasitoids. *Systematic Biology*.
- Brêthes, J. 1927. Nouveaux Hyménoptères parasites du Chili. *Revista Chilena de Historia Natural* 31: 194–200.
- Dowton, M., R. Belshaw, A. D. Austin and D. L. J. Quicke. In press. Simultaneous molecular and morphological analysis of braconid relationships (Insecta: Hymenoptera: Braconidae) indicates independent mt-tRNA gene inversions within a single wasp family. *Journal of Molecular Evolution*.
- Fischer, M. 1966. *Aspilodemon* ein neues Opiinen-Genus aus Brasilien (Hymenoptera, Braconidae). *Entomophaga* 11: 161–176.
- Fischer, M. 1968. *Kephalosema* ein neues Horniinen-



- Cephus* (Hymenoptera: Braconidae). *Polish Entomological Review* 38: 791–805.
- Gagliardi, P. J., R. A. M. Oda and R. F. Monteiro. 2001. The galls midges (Diptera: Cecidomyiidae) of *Mikania glomerata* (Asteraceae) in southeastern Brazil. *Proceedings of the Entomological Society of Washington* 103: 110–134.
- Infante, F., P. Hanson and R. A. Wharton. 1995. Phytophagy in the genus *Monitoriella* (Hymenoptera: Braconidae) with description of new species. *Annals of the Entomological Society of America* 88: 406–415.
- King, R. M. and H. E. Robinson. 1987. *The genera of Eupatoriaceae (Asteraceae)*. Missouri Botanical Garden, St. Louis. 581pp.
- Macêdo, M. V. de and R. F. Monteiro. 1989. Seed predation by a braconid wasp, *Allorhogas* sp. (Hymenoptera). *Journal of the New York Entomological Society* 97: 358–362.
- Marsh, P. M., M. V. de Macedo and M. C. P. Pimental. 2000. Descriptions and biological notes on two new phytophagous species of the genus *Allorhogas* from Brazil (Hymenoptera: Braconidae: Doryctinae). *Journal of Hymenoptera Research* 9: 292–297.
- Mori, S. A., B. M. Boom and G. T. Prance. 1981. Distribution patterns and conservation of eastern Brazilian coastal forest species. *Brittonia* 33: 233–245.
- Quicke, D. L. J., C. van Achterberg and H. C. J. Godfray. 1997. Comparative morphology of the venom gland and reservoir in opiine and alysiine braconid wasps (Insecta, Hymenoptera, Braconidae). *Zoologica Scripta* 26: 23–50.
- Quicke, D. L. J. and R. Belshaw. 1999. Incongruence between morphological data sets: an example from the evolution of endoparasitism among parasitic wasps (Hymenoptera: Braconidae). *Systematic Biology* 48: 436–454.
- Quicke, D. L. J. and T. Huddleston. 1989. The Australian braconid wasp subfamily Mesostoinae (Hymenoptera: Braconidae) with the description of a new species of *Mesostoa*. *Journal of Natural History* 23: 1309–1317.
- Ramirez, W. B. and P. M. Marsh. 1996. A review of the genus *Psenobolus* (Hymenoptera: Braconidae) from Costa Rica, an inquiline fig wasp with brachypterous males, with description of two new species. *Journal of Hymenoptera Research* 5:64–72.
- Ritter, M. R., L. R. M. Baptista, and N. I. Matzenbacher. 1992. Asteraceae gênero *Mikania* Willd Seccões Globosae e Thirsigeriae. *Boletim do Instituto de Biociências / UFRGS* 50: 1–90.
- Sharkey, M. J. and R. A. Wharton. 1997. Morphology and terminology. In R. A. Wharton, P. M. Marsh & M. J. Sharkey (eds) *Identification manual to the New World genera of Braconidae*. Special Publication of the International Society of Hymenopterists 1: 19–37.
- Shaw, M. R. and T. Huddleston. 1991. Classification and biology of braconid wasps (Hymenoptera: Braconidae). *Handbooks for the Identification of British Insects* 7(11): 1–126..
- Shaw, M. R. and D. L. J. Quicke. 2000. The biology and early stages of *Acampsis alternipes* (Nees), with comments on the relationships of the Sigalphinae (Hymenoptera: Braconidae). *Journal of Natural History* 34: 611–628.
- Wharton, R. A. 1988. Classification of the braconid subfamily Opiinae (Hymenoptera). *The Canadian Entomologist* 120:333–360.
- Wharton, R. A. 1993. Review of the Hormiini (Hymenoptera: Braconidae) with a description of new taxa. *Journal of Natural History* 27: 107–171.
- Whitfield, J. B. and R. A. Wharton. 1997. Subfamily Hormiinae. In R. A. Wharton, P. M. Marsh and M. J. Sharkey (eds) *Identification manual to the New World genera of Braconidae*. Special Publication of the International Society of Hymenopterists 1: 285–301.